

Differential Feeding Behaviour of the Sympatric Hyrax *Procavia johnstoni* and *Heterohyrax brucei**

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Summary. 1. It has been reported that when the vegetarian Bush hyrax *Heterohyrax* and the Rock hyrax *Procavia* are allopatric they occupy an almost identical niche, while when sympatric they differ in feeding behaviour. To investigate whether indeed a displacement in feeding behaviour takes place where *Procavia johnstoni* and *Heterohyrax brucei* occur sympatrically, the feeding characteristics of three (two *H. brucei*, one *P. johnstoni*) allopatric family groups and four (two of each species) sympatric family groups living on five kopjes in the Serengeti were studied and compared.

2. The vegetation of these five kopjes was surveyed. It was divided into four classes (grass, forb, bush, tree), the plant species identified and the indices of diversity and similarity calculated. The plant biomass was roughly quantified through a foliage density (f. d.) factor and the seasonal variation of vegetation recorded.

The number of plant species ranged from 65 to 95 (Fig. 4). The closer the kopjes are geographically, the greater the resemblance in their plant species composition (Fig. 6). Although bushes and trees comprise the fewest plant species (15–27%) they form the highest foliage density values (65–85%; Table 1, Fig. 5). There is a substantial variation of plant species diversity. A significant correlation exists between the diversity indices and crown cover, but there is no correlation between diversity indices and a) kopje area or b) the quotient of total number of hits per transect length.

Grasses, forbs and small bushes observe more or less the rainfall pattern, while other bushes, and trees, never completely lose their leaves (Fig. 7).

3. The behaviour of individuals in the groups was regularly observed and recorded in the wet and dry seasons.

a) *H. brucei* was observed feeding on 64 plant species (Annex A) but 2–11 species formed 90% of the animals' staple diet. There is a high correlation ($r_s = 0.90$) between the comparative abundance of vegetation (measured by f. d.) and the proportions of the four vegetation classes eaten by *H. brucei* (Fig. 8). All four family groups fed roughly in proportion to the foliage density, yet showed preference for certain plant species. They browsed predominantly on bushes and trees in the wet (81%) and dry (92%) seasons (Fig. 11), but showed a tendency to eat more grass and browse less in the wet season. There are marked differences in feeding between the family groups, due to selective preferences and the vegetation composition in the respective kopjes (Table 2, Fig. 10).

b) *P. johnstoni* was observed feeding on 79 plant species (Annex A). The animals have a high seasonal adaptability: in the wet season they showed a high preference for grasses (78%), but in the dry season when grasses became parched and poor in quality they browsed (57%) extensively (Fig. 11), and more or less in proportion to the foliage density of each vegetation class (Fig. 9).

P. johnstoni must go outside the kopje to graze. Around one kopje the cropped grass area was very marked, its size varying with rainfall (Figs. 12 and 13).

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c) Competition for food could occur especially in the dry season when both species browse. However, no evidence could be found for a competition-induced displacement here.

4. Almost no aggressive behaviour was observed between the species.

5. Both *P. johnstoni* and *H. brucei* have morning and evening feeding activity peaks in the wet and dry seasons, the evening one always being higher (Fig. 14). There was no indication in sympatric groups of any activity shift induced by the presence of the other species.

Evidence on the social character of group feeding and the guarding function of the territorial ♂♂ is presented.

6. The results obtained are compared with those of other authors. There is no indication of niche segregation in sympatric kopjes. Possible climatic and other reasons for regional sympatry are discussed.

The advantage of selecting food items rich in protein and energy and low in fibre content are considered and food competitors listed.

Introduction

In the Serengeti National Park the Rock hyrax *Procavia johnstoni matschiei* Neumann 1900 and the Bush hyrax *Heterohyrax brucei dieseneri* (Vic. njansae) Brauer 1917 (Fig. 1) live together on some rock outcrops or kopjes (Fig. 2) and utilize essentially the same resources.

Whenever two closely related species use the same limited resources in the same location, the more efficient species may eventually completely exclude the other (Hardin, 1960); or both species may coexist, e.g. by reason of heavy predation pressure, which may partially suspend the effects of competition (Roughgarden and Feldman, 1975), or because of character displacement (Brown and Wilson, 1956). Such ecological separation of sympatric species may be due to the occupa-



Fig. 1. Association of Bush hyrax (*Heterohyrax brucei*) and Rock hyrax (*Procavia johnstoni*): the two smaller animals in front are adult Bush hyrax, the others are adult Rock hyrax

1. Berichterstatter: J. Jacobs
 2. Berichterstatter: W. Wickler
 Tag der mündlichen Prüfung: 7.7.75

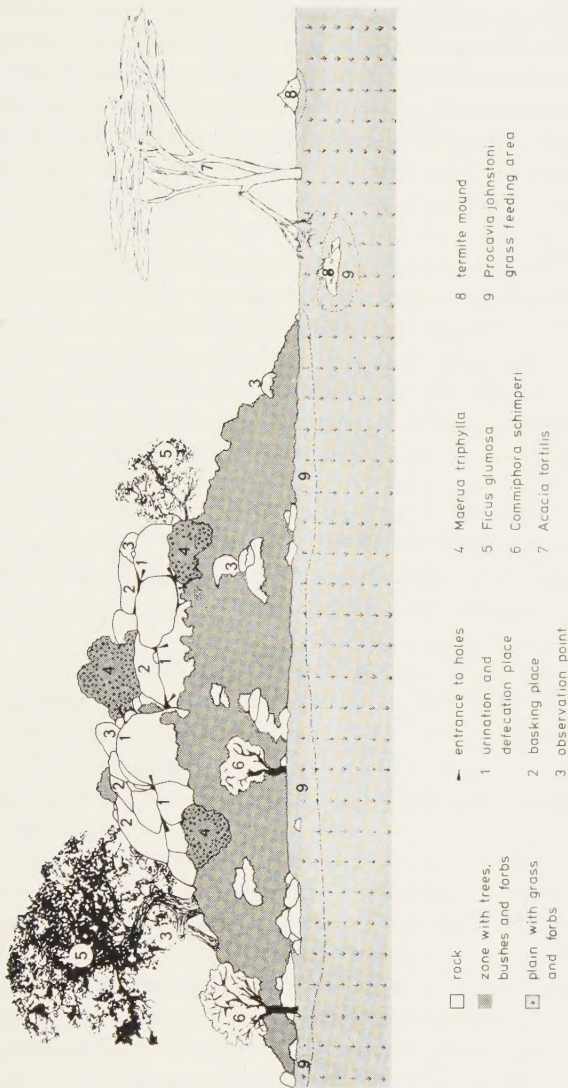


Fig. 2. Schematic drawing of a kopje (PH 1 slightly simplified) with characteristic vegetation and features relevant for the hyrax

tion of different habitats in the same area or to difference in feeding, as occurs in birds (Lack, 1971). Also behavioural interactions may cause the ecological separation of species, as is known from several studies on sympatrically occurring rodent species, where social dominance between species plays an important role in habitat selection (Brown, 1971; Cameron, 1971; Heller, 1971; Stoecker, 1972; Hoffmeyer, 1973; Morse, 1974). The question arises, which mechanisms enable Rock and Bush hyrax to coexist on the kopjes in the Serengeti?

Turner and Watson (1965) made a first ecological study on a kopje where *P. johnstoni* and *H. brucei* coexist. They observed that *P. johnstoni* is an almost exclusive grazer, while *H. brucei* is an exclusive browser. They write: "In respect of feeding therefore the two species of hyrax cohabiting many kopjes in the

Serengeti are completely separated, whereas in many other activities they are indistinguishable". On the other hand Sale (1965a, b, 1970a) found that in Kenya the allopatrically occurring *P. habessinica* (which is similar in many ways to *P. johnstoni*) and *H. brucei hindei*, have basically similar social behaviour and occupy an almost identical niche. These results strongly suggest the possibility of ecological displacement with respect to feeding behaviour, and thus a niche segregation whenever the two hyrax species *P. johnstoni* and *H. brucei* occur sympatrically.

To investigate whether in fact such a displacement exists, I compared the feeding characteristics of allopatric groups of each species with those of sympatric groups in the Serengeti. The present study is divided into two sections: the first describes the kopje vegetation, and food preferences of four *H. brucei* and three *P. johnstoni* family groups in the wet and dry seasons, the second describes briefly some behaviour patterns related to feeding. A more detailed account of the latter will be given in a publication on the social behaviour of the hyrax, which is in preparation.

General Biology of the Hyrax

The Hyrax (Order *Hyracoidea*) belong together with the Elephants (Order *Proboscidea*) and the Seacows (Order *Sirenia*) to the Super-Order of the *Paenungulata* or "nearly ungulates" (Simpson, 1945).

One can distinguish three Genera restricted to Africa and the Middle East (Hahn, 1959; Bothma, 1966; Kingdon, 1971). The nocturnal arboreal Tree hyrax *Dendrohyrax* inhabits the forests, while the diurnal Bush hyrax *Heterohyrax* and the Rock hyrax *Procavia* live in a rocky habitat. *Heterohyrax* can also be found in trees, while *Procavia* has the widest distribution, invading the driest and highest areas.

In a comparison of the two studied species, differences in size are immediately evident (Fig. 1): 60 adult *P. johnstoni* had a mean body weight of 3.14 ± 0.60 kg (standard deviation), while 121 adult *H. brucei* had a mean body weight of 1.79 ± 0.26 kg (st. dev.).

According to Sale (1965a) and Meltzer (1967) hyrax appear to live in family groups. My own observations have shown (Hoeck, in prep.) that the basic family structure of *P. johnstoni* and *H. brucei* consists of one adult territorial ♂, several adult ♀♀ and the youngsters of both sexes. In kopjes of small area, where only one family group is found, pubescent ♂♂ are driven out by the territorial ♂. The social relations in large kopjes harbouring more than one family group are still unknown.

Definite breeding periods occur generally at the end of the wet season, in the months April-June, but they may vary between different kopjes or kopje groups. Up to four, usually two young are born after a gestation period of approximately $7\frac{1}{2}$ months (Roche, 1962; Mendelssohn, 1965; Sale, 1965c). On those kopjes where Rock and Bush hyrax occur sympatrically they share the same living holes, use the same urination and defecation places, bask together and have similar feeding periods. Several authors report on feeding behaviour, and on the food items eaten by hyraxes in studies on animals in captivity (Bruce, 1790; Hahn, 1959; Rahm, 1964; Mendelssohn, 1965; Sale, 1966b; van Doorn, 1972) and from

chance observations on expeditions (Burton, 1824, in Flower, 1932; Hauser, 1951). More intensive field studies have been made by Coe (1962), Sale (1965a, b), Turner and Watson (1965) and Meltzer (1967). These studies show that the hyrax is a vegetarian and comprehensive feeder, eating from a wide variety of the vegetation available. Sale (1965a, b) reports that 89 plant species from lichens to trees supply food for *P. johnstoni mackinderi*, *H. brucei hindei* and *P. habessinica* in Kenya. Meltzer (1967) observed *P. capensis syriaca* feeding on 44 plant species in Israel. Coe (1962) found a preponderance of grass and moss material in the stomach of *P. j. mackinderi*. Hahn (1959), Sale (1965b) and Meltzer (1967) report that food preference is seasonal, plants with tender new shoots, buds and leaves being eaten in the wet season, while in the dry season when these fail the animals feed on coarser vegetation and even on bark.

Sale (1965b), Turner and Watson (1965) and Meltzer (1967) report that *Procavia* and *Heterohyrax* are diurnal and that feeding occurs mainly in the morning and evening. Restriction of feeding activity to the cooler hours of the day is probably due to the poor homeothermal regulation of body temperature (Taylor and Sale, 1969; Bartholomew and Rainey, 1971). Sale (1965a, b) describes two types of feeding; group feeding, having two very distinct daily maxima involving all or most of a family group, a lot being consumed in a short time, and casual feeding involving single animals eating at any time of the day.

The Study Area

The field studies were conducted from 1971 to 1973 in the Serengeti National Park, Tanzania. The majority of the observations were made on kopjes relatively close to the Serengeti Research Institute, located in the marginal area between woodlands and grass plains at around 1250 m altitude (Fig. 3). Detailed descriptions of the Serengeti ecosystem are given in several recent publications (Anderson and Talbot, 1965; Hendrichs, 1970; Bell, 1971; Braun, 1972; Kruuk, 1972; Schaller, 1972; Sinclair, 1974).

1. Climate

Mean annual rainfall varies from 600 to 800 mm. The seasons are somewhat erratic but the dry season is usually June–October and the wet season November–May, with a precipitation peak in March–April. In the dry season there are long spells without rainfall save for occasional thunderstorms, easterly winds, great temperature fluctuation between day and night, and frequent fires in the plains. In the wet season winds are irregular and their direction varies, there is more cloud cover throughout the day, heavy rains to occasional constant drizzle and less variation of day/night temperature.

2. The Kopje

The kopjes are granite, grandiorite and gneiss rock outcrops (Anderson and Talbot, 1965) protruding like islands from the surrounding plains to an elevation of up to 30 m (Fig. 2). Most kopjes in the National Park are clustered, forming several separate kopje groups (Fig. 3).

Heavy erosion by wind and water, and the great temperature fluctuation have led to the building on these islands of a very heterogenous topography in the form of crevices, fissures, holes and caves. The lower slopes of some kopjes are heaped with rock and boulder debris split off by temperature changes and forming screens.

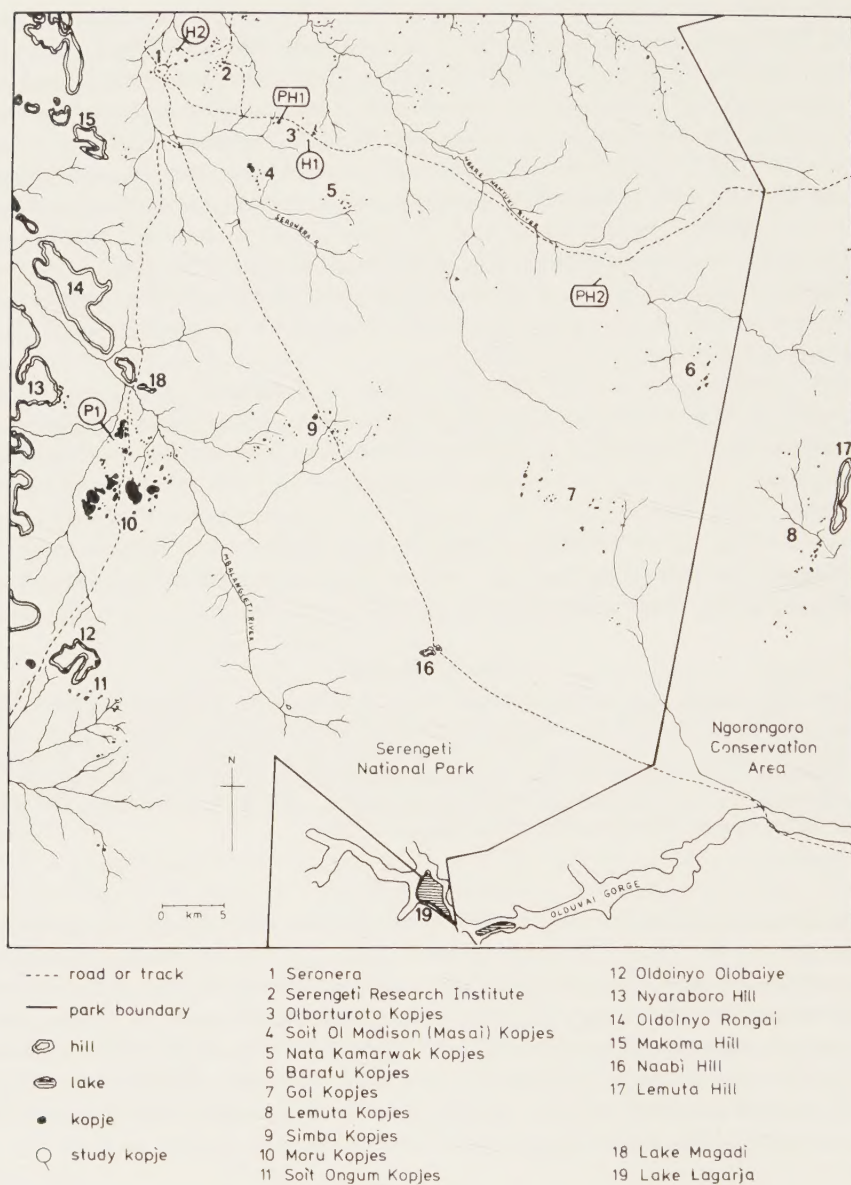


Fig. 3. Map of the southeastern part of the Serengeti National Park showing the different kopje groups and the five kopjes under study

3. Kopje Vegetation

The vegetation of most kopjes is rich in herbs, bushes and trees, and is strikingly different from the vegetation of the surrounding plains. This difference may be due to several factors, such as the heterogenous kopje topography, the concen-

tration of organic and inorganic matter in fissures and round the kopje base, and the vegetation being less exposed to fire. The bulk of the vegetation consists of bushes and trees covering the deposits on the lower kopje slopes (Fig. 2) between the edge of the grassland community and the higher kopje rock. Growth on the kopje top is usually more sparse, but single shrubs or trees often root in fissures.

4. The Kopje as Hyrax Habitat

The abundant, dense vegetation cover and the heterogenous topography form an ideal habitat for the hyrax, which are the most characteristic resident mammals.

Fissures and holes, having nearly constant temperature and humidity, provide living quarters for the animals as well as shelter. Outside, the vegetation affords the necessary cover from the many predators, mainly eagles, and a good food supply throughout the year. Each rain shower leaves pools in rock concavities, and possibly lasting water pockets form in deep fissures within the kopjes, providing drinking water even in the dry season.

Kopjes are occupied by either *P. johnstoni* or *H. brucei* or both species, with the exception of the groups in the south-eastern part of the Park (Simba, Gol and Barafu Kopjes; Houston, 1967). Either the animals failed to reach them, or the vegetation is insufficient to support hyrax, as these kopjes lie in the drier part of the Park. Another reason may be that most of these kopjes had at one time been denuded by pastoralists (Schaller, 1972).

5. The Kopjes Studied

Five kopjes were studied (see Table 1 and Fig. 3), which were selected from the following aspects:

a) to be isolated from other kopjes, and small enough to allow trapping and individual marking of all animals, so that population dynamics and social behaviour could be studied, and

b) having not too dense vegetation, but an "even topography", so that the small animals could more easily be seen.

The letters "P" and "H" signify kopjes with *P. johnstoni* or *H. brucei* respectively, while "PH" indicates the presence of both species.

Kopje H 1: formed by two small outcrops in the Olborturoto Kopje group. Their areas are 2047 and 1565 m², they are about 6 m high and lie 40 m apart. One *H. brucei* family group consisting of 1 adult ♂, 5-6 adult ♀♀ and 8-12 juveniles occupies and regularly moves between them.

Kopje H 2: a small kopje about 4 m high close to a stream separating it from the Seronera Parks Camp. Here an *H. brucei* family group of 1 adult ♂, 2-4 adult ♀♀ and 3-5 juveniles lives.

Kopje P 1: a small outcrop about 8 m high of the Moru Kopjes, some 60 km south of the Institute. This kopje harbours one *P. johnstoni* family group of 1 (for 6 months 2) adult ♂, 2-3 adult ♀♀ and 3-10 juveniles.

Kopje PH 1: like H 1, one of the Olborturoto Kopje group, having the biggest area of those studied, and consisting of a main kopje about 12 m high with several adjacent ones; it is inhabited by one *P. johnstoni* group of approx. 22 animals, and one *H. brucei* group of approx. 45 animals.

Table 1. Basic characteristics for the five kopjes studied. The kopje area and crown cover b were calculated from aerial photographs. The mean annual rainfall (standard deviation in brackets) represents data from Wotro and Serengeti Ecological Monitoring Program. Diversity indices (S , H' , E) are calculated from plant species with foliage density values above 3%. For further details see text

Kopje	H 1	H 2	PH 1	Photo-graphed section	PH 2	P 1
Area (m ²)	3612	2806	10046	2588	2036	2495
Mean annual rainfall (mm)	575.9 (151.8)	855.7 (184.8)	575.9 (151.8)		478.2 (190.4)	695.5 (229.9)
Ground measurements						
Transect length (m)	558.5	261.0	437.5	307.0	254.5	430.5
Total no. of hits	1326	435	951		360	446
Foliage density						
Grass (%)	22.7	28.6	12.6		19.2	27.8
Forb (%)	1.7	5.9	1.7		10.0	
Bush (%)	34.8	59.9	43.1		6.9	71.0
Tree (%)	40.8	5.6	42.6		63.9	1.2
Crown cover a (%)	44.1	18.8	52.2	57.1	20.0	21.2
Crown cover b (%)	39.9	14.2		50.0	19.4	19.6
b/a	0.90	0.76		0.88	0.97	0.92
No. of species S	13	4	8		6	7
Diversity H'	2.45	0.86	1.87		1.26	1.70
Evenness E	0.96	0.62	0.90		0.70	0.88

Kopje PH 2: having an area of and a height of about 8 m, located 60 km east of the Institute on the short grass plains. No hyrax lived on this kopje. Six animals (2 ♂♂, 4 ♀♀) of each species were introduced in September 1971.

Methods

1. Vegetation

A detailed survey was made of the plant species composition of each kopje, which was then compared with that of every other kopje, applying the *Index of Similarity* (Sørensen, 1948) $s' = (2C)/(A+B)$, where A = number of species in kopje A , B = number of species in kopje B , and C = number of species in common to both kopjes.

The vegetation was divided into four classes: *grasses* (families *Gramineae* and *Cyperaceae*), *forbs* (families *Agavaceae*, *Liliaceae* and all non-woody dicotyledons; term adopted from Hofmann and Stewart, 1972), *bushes* and *trees*. Kopjes H 1 and PH 1 vegetation was measured in May 1971, kopjes PH 2 and P 1 in January 1972 and kopje H 2 in November 1972, using the point analysis technique (Brown, 1954). For various reasons, such as tourist disturbance and lack of time, the vegetation was measured only once.

Six to eight parallel transects were mapped out with a tape measure at regular intervals across each kopje. A cm measuring rod was held vertically every 50 cm. Each hit was recorded,

that is, each point at which a plant species touched the rod. If two or more hits were recorded for the same plant, maximum and minimum heights were noted.

The foliage density factor for a given plant species or class was calculated by adding the distances between all maximum and minimum hits in a kopje. A plant touching once only was calculated as a distance of 1 cm. The species values were expressed in percentages of the total sum of values of all species in a kopje.

All transects were taken to 3–5 m from the kopje edge into the surrounding grass. In this zone the bush/forb/stone community gives way to the grass/forb community. Usually the animals (*P. johnstoni* especially) feed within 3–5 m of the kopje edge. Because of the arbitrariness of the outer kopje limit, the values for grass density are debatable.

The crown cover *a* was calculated from the frequency that bushes and trees hit the rod and then expressed in percentage of the total kopje area. For comparison the crown (*b*) cover was also calculated by the dot sampling technique (Loetsch and Haller, 1964) from aerial photographs. Because of the large area of kopje PH 1 only a section of the kopje was photographed and compared with the corresponding transects of ground measurement.

The third line before the last of Table 1 gives the quotients (equality = 1) between both methods of measurement. With the exception of kopje H 2 the quotient values are close to unity, indicating that there is a fair correspondence between the methods. The aerial photograph of H 2 was taken at a slight angle.

The *Indices of Diversity and Evenness* were calculated for each kopje from the species foliage density values above 3%, by applying the equations: $Diversity\ H' = \sum \left(\frac{n_i}{N} \right) \log_e \left(\frac{n_i}{N} \right)$, where n_i = the foliage density of the i^{th} species, N = the total foliage density of all species. *Evenness* (Pielou, 1966) $E = (H')/(\log_e S)$, where S = number of species.

In calculating correlations, Spearman's rank correlation coefficient r_s (one-tailed test) was used.

Fluctuations of kopje vegetation were noted every 4 weeks for a period of 2 years. Grass was recorded as short, medium or long; dry, half-green or green. Bush and tree leaf cycles were recorded in a subjective scale from 0 (no leaves) to 10 (full leaf). Flower and fruit were recorded whenever observed.

2. Climate

Temperature and relative humidity were recorded daily with a thermohydrograph placed on a kopje top in a perforated white wooden box. These readings may be influenced by rock radiation and other factors, and should be regarded as approximate.

For calculating food preferences, any month showing rainfall less than 50 mm was defined as a dry season month, any month with more was defined as a wet season month.

3. Animal Observations

Four *H. brucei* and three *P. johnstoni* family groups were observed on five kopjes.

All observations were made from a Land Rover standing 10–50 m from the kopje, depending on the timidity of the particular family group. Because of the distance and the size of the animals binoculars had to be used throughout. Nearly all animals were trapped, weighed, individually marked and released again at least annually. In kopje PH 1 not all animals could be trapped. Observations were made mainly in 3-hr periods during the two feeding activities but also in 6- and 12-hr periods during daylight.

The behaviour of each animal seen was recorded on a check sheet in momentary observations at regular 3 min intervals. Recorded were behaviour patterns such as lying, walking, feeding of each animal as well as intraspecific and interspecific interactions (aggression, play, etc.) between individuals. The position of each individual was plotted on a map every ten minutes.

If an animal was feeding, the plant species was noted. For each family group the sum of observation units was taken as 100% and the percentage of feeding time for each vegetation class or plant species calculated. The χ^2 test for two independent samples (2×2 contingency table) was used to demonstrate the feeding differences in *grazing* (eating exclusively plant

species of the grass class) and *browsing* (forb, bush and tree-eating) for each season, by comparing each family group with every other family group.

An attempt was made to assess the monthly grass biomass consumed by the *P. johnstoni* family group of kopje P 1. Unfortunately most of the grass exclosures were regularly trampled by elephants and giraffes, so that data collected was unreliable.

A small group of tame but free-living *P. johnstoni* (4–6 animals) and a large relatively tame *H. brucei* (40–50 animals) group living sympatrically on two kopjes close to the author's quarters were also observed. As these animals could be observed fairly easily, data showing the daily course of feeding activity for the wet and dry seasons was taken from these groups. Here recordings were made in 5 min momentary observations for 6 hrs daily.

The values of the ordinate in Fig. 14 were calculated from the mean number of animals seen feeding in 5 min momentary observations for every hour of the day. This value was then divided by the total number of animals in the family group. No night feeding was observed, not even during three moonlight nights.

Results

A.1. The Kopje Vegetation

A.1.1. Plant Species Composition and Similarity between Kopjes

Altogether 196 plant species were recorded; the number collected per kopje ranged from 65–95, as shown in Fig. 4, the majority grasses and forbs.

There is a fair degree of similarity among the kopjes. The similarity indices range from 0.30 to 0.53 (Fig. 6).

The closer the kopjes are geographically, the greater the resemblance in their plant species composition. The relation between the index of similarity and the distance between kopjes shows a high correlation ($r_s = 0.76$, $P < 0.01$).

A.1.2. Foliage Density and Crown Cover in the Five Kopjes

The foliage density (f.d.), crown cover (c.c.) and the diversity indices (S , H' , E) are given in Table 1; plant species composition is shown in Fig. 5.

There is a substantial variation of plant species diversity when foliage density exceeds 3%; it is greatest in kopje H 1 (number of species $S = 13$, diversity $H' = 2.45$, evenness $E = 0.96$) and lowest in H 2 ($S = 4$, $H' = 0.86$, $E = 0.62$). The rank order H 1, PH 1, P 1, PH 2, H 2 is constant for all three diversity indices. There is a significant correlation between diversity indices and crown cover ($r_s = 0.90$, $P = 0.05$), but none ($r_s = 0.60$, $P > 0.05$) between diversity indices and either kopje area or the quotient of the total number of hits per transect length.

Although bushes and trees account for only 15–27% of plant species (Fig. 4), they form most of the plant biomass of the kopje. Their predominance is expressed in their high values, ranging from 65–85%, of the total kopje foliage density; also the crown cover values of 19–52% demonstrate this dominance if one considers that for this calculation the rock and soil area of the kopje is included in the total area.

Marked differences are found between the kopjes. But kopjes PH 1 and H 1 have a similar bush and tree composition covering about half the areas (PH 1: c.c. 52%; H 1: c.c. 44%), the bush *Hoslundia opposita* and the trees *Ficus glumosa* and *Ficus ingens* accounting for most of the foliage density (Fig. 5).

Kopje H 2 is sparsely covered (c.c. 19%). Of the total foliage density 58% consists of the bush *Grewia fallax*. Trees are of minor importance.

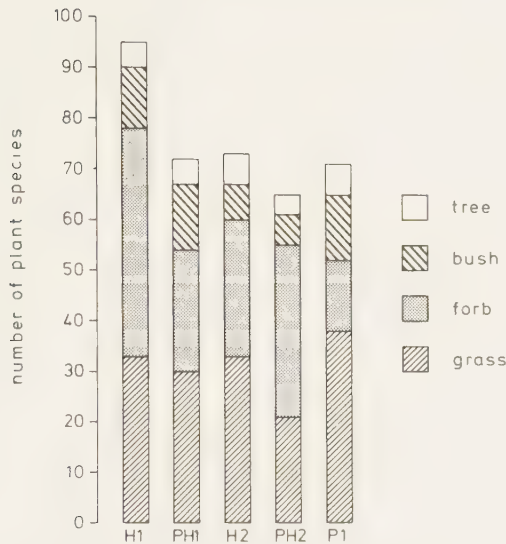


Fig. 4. Number of plant species of the four vegetation classes found on the five kopjes studied

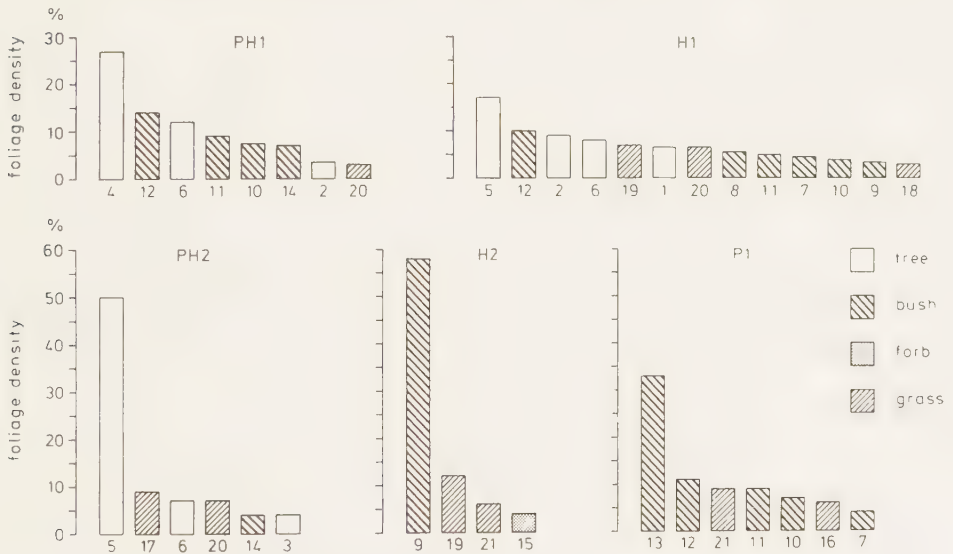


Fig. 5. Plant species foliage density of the four vegetation classes (values above 3%) for the five kopjes. 1 *Acacia tortilis*; 2 *Commiphora schimperi*; 3 *Commiphora merkeri*; 4 *Ficus glumosa*; 5 *Ficus ingens*; 6 *Maerua triphylla*; 7 *Allophylus rubifolius*; 8 *Cordia ovalis*; 9 *Grewia fallax*; 10 *Grewia trichocarpa*; 11 *Hibiscus lunariifolius*; 12 *Hoslundia opposita*; 13 *Iboza* sp.; 14 *Pavetta assimilis*; 15 *Sansevieria ehrenbergiana*; 16 *Bothriochloa insculpta*; 17 *Cynodon dactylon*; 18 *Digitaria velutina*; 19 *Panicum maximum*; 20 *Pennisetum stramineum*; 21 *Themeda triandra*

Kopje PH 2 also has thin bush and tree cover (c.c. 20%), the major foliage density values being contributed by the trees *Ficus ingens*, *Maerua triphylla* and *Commiphora merkeri* and the grasses *Cynodon dactylon* and *Pennisetum stramineum*. Few bushes, but some *Pavetta assimilis*, grow on this kopje.

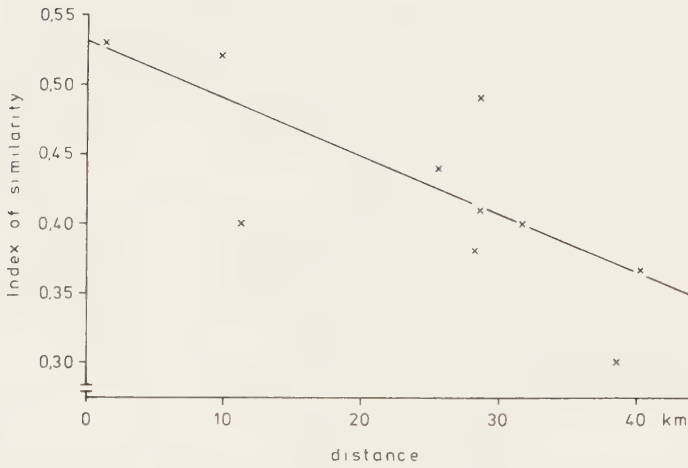


Fig. 6. Correlation between index of similarity and the distance between the studied kopjes (Regression line $y = -0.004x + 0.53$)

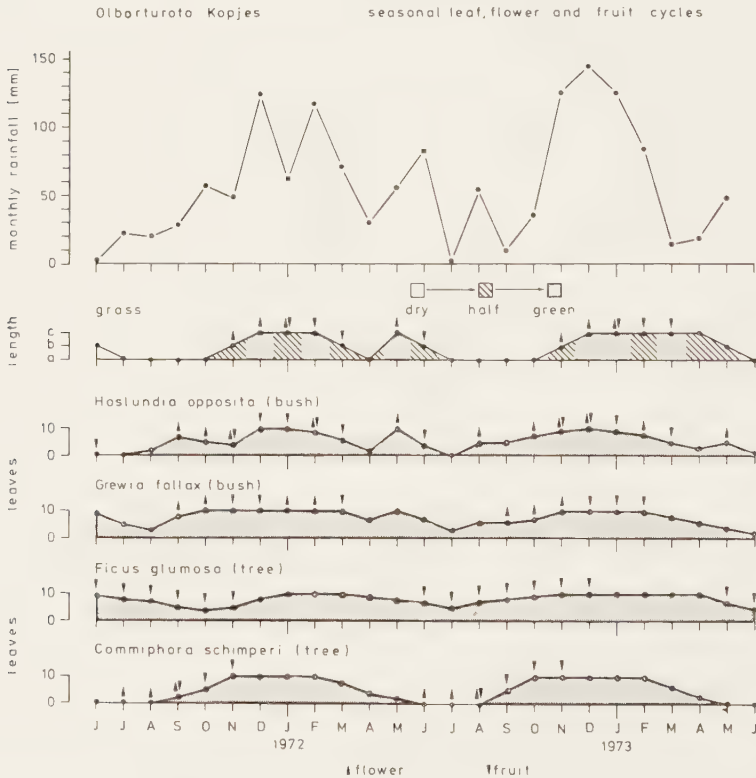


Fig. 7. Olborturoto Kopje group (kopjes H 1 and PH 1): the monthly rainfall (data from Wotro and Serengeti Ecological Monitoring Program) and the seasonal leaf, flower and fruit cycles for some typical plant species over a 2-year period (June 1971 to June 1973). Grass was recorded as short (a), medium (b) or long (c); dry, half-green or green. Bush and tree leaf cycles were recorded in a subjective scale from 0 (no leaves) to 10 (full leaf). Flower and fruit were recorded whenever observed

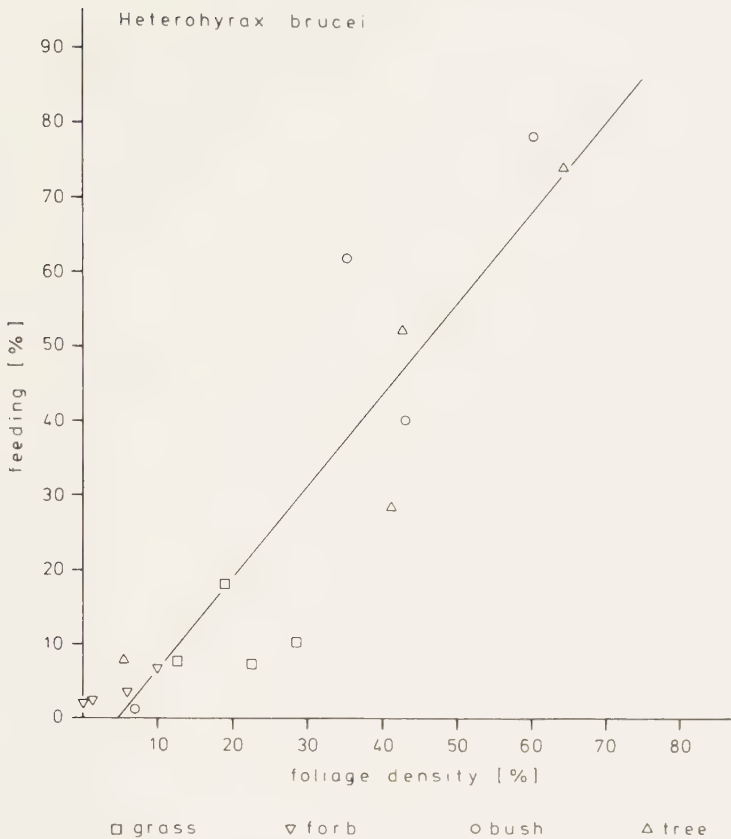


Fig. 8. Foliage density percentage of the four vegetation classes (see Table 1) and feeding in percentage (mean values of dry and wet season) of the four *H. brucei* family groups. Vegetation consumed by *H. brucei* is shown to be roughly in proportion to amounts available (regression line $y = 1.2x - 5.9$)

In P 1 the crown cover of 21% consists mainly of the bushes *Iboza* sp., *Hoslundia opposita* and *Hibiscus lunarifolius*. Trees are of minor importance.

A.1.3. Seasonal Leaf, Flower and Fruit Cycles

Fig. 7 shows the seasonal leaf, flower and fruit cycles of some of the more important plant species of kopjes H 1 and PH 1. The examples were chosen in order to demonstrate the most typical growth patterns.

Grasses and forbs, and small bushes such as *Hoslundia opposita*, *Hibiscus lunarifolius*, *Iboza* sp., more or less observe the rainfall pattern. They grow rapidly and foliate after the first rains, stop growth and shrivel or drop their leaves soon after the rains stop.

Deep-rooted bushes such as *Grewia fallax*, *Grewia trichocarpa*, *Cordia ovalis*, *Pavetta assimilis*, or trees such as *Ficus glumosa*, *Maerua triphylla* never completely lose their leaves, even continuing to produce them far into the dry season.

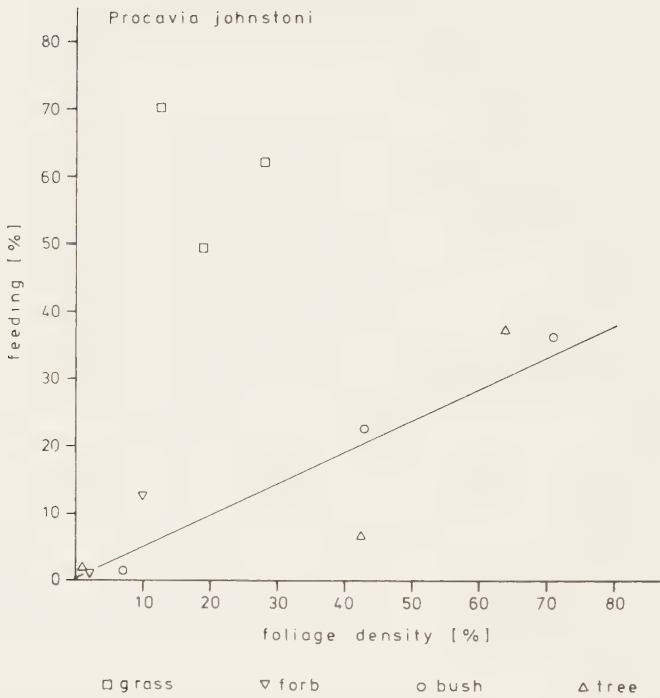


Fig. 9. Foliage density percentage of the four vegetation classes and feeding percentage of the three *P. johnstoni* family groups. Browse material (forb, bush and tree) is consumed roughly in proportion to amounts available (regression line without grass $y = 0.48x + 0.31$). *P. johnstoni* shows a great preference for grasses

Some plants, such as the tree *Commiphora schimperi*, follow a fixed annual periodicity independent of minor rainfall fluctuation.

A.2. Food Preference

A.2.1. Food Preference of the Individual Family Groups

a) *H. brucei*. *H. brucei* was observed feeding on 64 different plant species as listed in Appendix A.

Table 2 lists plant species predominantly eaten by the various family groups in both seasons. Depending on the kopje vegetation and the season 90% of the animals' staple diet was formed by 2-11 plant species.

In Fig. 8 are plotted the foliage density percentages of the four vegetation classes and the feeding percentages of the four family groups. The feeding percentages are mean values for the wet and dry seasons.

There is a high correlation ($r_s = 0.90$, $P < 0.01$) between the proportions of the four vegetation classes eaten by *H. brucei* and the vegetation distribution as measured (foliage density) in the kopje. The regression line is close to unity: the animals fed roughly in proportion to the vegetation present.

Table 2. Percentages foliage density (Fd) and percentage of time moments the animals (Het = *H. brucei*, Pro = *P. johnstoni*) were seen feeding on various plant species in the dry season and (in brackets) the wet season. Feeding values below 1% are omitted. The listed plant species are characteristic for the kopje vegetation and form the animals' staple diet. The one grass species given grows only in the kopje or in its immediate surroundings

Plant species	Kopje PH 1			Kopje PH 2			Kopje H 1		Kopje H 2		Kopje P 1	
	Fd (%)	Het (%)	Pro (%)	Fd (%)	Het (%)	Pro (%)	Fd (%)	Het (%)	Fd (%)	Het (%)	Fd (%)	Pro (%)
Grass:												
<i>Panicum maximum</i>	2	1	9			(1)	7	2 (2)	12	5 (4)	3	
Bush:												
<i>Cordia ovalis</i>	2	2 (18)	(3)				5	38 (33)	—			
<i>Grewia fallax</i>	—			—			3	2 (5)	58	73 (75)		
<i>Grewia trichocarpa</i>	8	4		—			4	7		7 (2)		
<i>Hibiscus lunariifolius</i>	9	23 (7)	25	—			5	11 (15)	—		9	6 (3)
<i>Hoslundia opposita</i>	14	2 (14)	7 (7)	—			10	5 (4)	—		11	1 (3)
<i>Iboza</i> sp.	—			—			—		—		33	47 (5)
<i>Pavetta assimilis</i>	7	11		4	1 (1)	1 (2)	2		—			
Tree:												
<i>Acacia tortilis</i>		2		—			6	5 (8)			—	
<i>Commiphora schimperi</i>	4	5					9	4	2	5 (4)		
<i>Commiphora merkeri</i>	—			4	(7)		—		—			
<i>Ficus glumosa</i>	27	12 (2)	3	—			—		—		—	
<i>Ficus ingens</i>	—			50	65 (16)	23 (5)	17	9 (5)	—		—	
<i>Maerua triphylla</i>	12	25 (52)	10	7	25 (36)	28 (19)	8	11 (7)	—			
Total	85	87 (93)	54 (10)	65	91 (60)	52 (27)	76	94 (79)	72	90 (85)	56	54 (11)

There were certain *seasonal differences* in food preferences. Fig. 10 gives the feeding percentages for both seasons and the foliage density percentages for the four classes of vegetation as in Table 1.

In each kopje the animals browsed mainly, which reflects the fact that bushes and trees predominated (*cf.* Fig. 8).

There was a tendency to feed more on grass and less on bushes and trees in the wet than in the dry season. For the family groups on kopjes H 1 and PH 2 this difference in *grazing* and *browsing* proportions between the wet and dry seasons is significant ($P < 0.001$, $df = 1$; $\chi^2 = 26$ and $\chi^2 = 159$, respectively). This was not observed for H 2 and PH 1.

Also *between the family groups* significant differences in feeding were observed: in the wet season between PH 2 and PH 1, PH 2 and H 1, PH 2 and H 2, and in the dry season between PH 2 and PH 1, PH 2 and H 2, PH 1 and H 1, H 2 and H 1 (see Table 3).

There are two causes that may explain these group differences:

a) Difference in *vegetation composition* between kopjes. For instance, kopjes PH 1 and H 1 provided a rich variety of bush and tree species (see also Fig. 5) which were browsed in different proportions. A *Cordia ovalis* bush in the middle

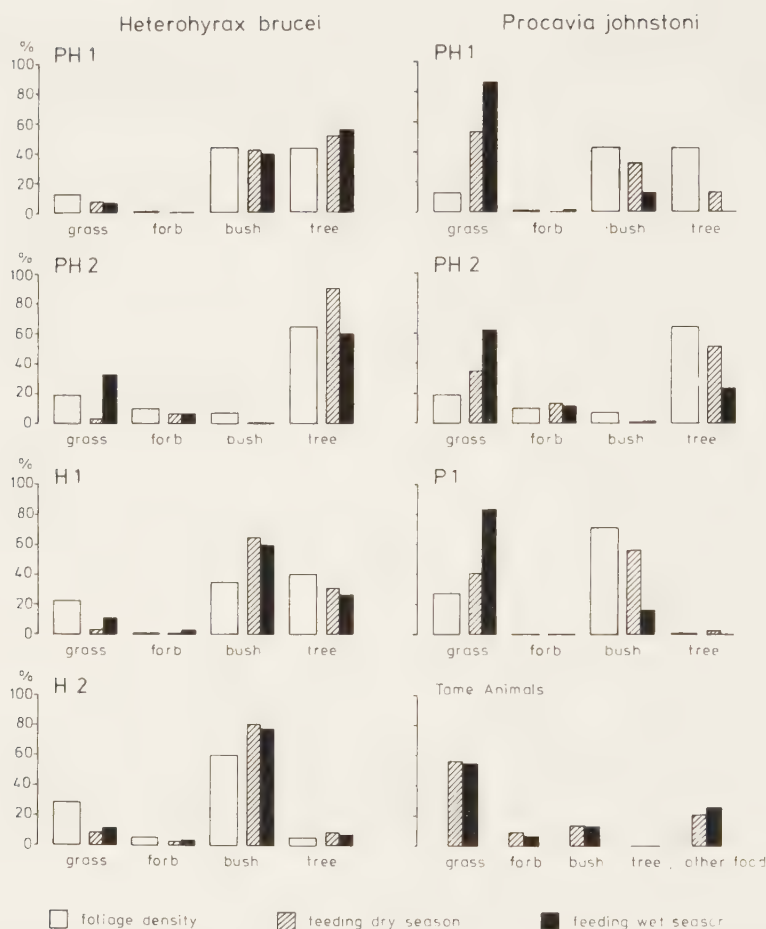


Fig. 10. Foliage density (see Table 1) and feeding in percentages in the dry and wet season for *H. brucei* and *P. johnstoni* in each kopje. Each group of four columns representing a season equals 100%. Feeding values of the tame free-living animals are also given. "Other food" means bananas, oats etc. For this kopje the foliage density was not calculated

of one of the small H 1 kopjes formed more than 30% of the animals' diet in both seasons (Table 2).

On kopjes PH 2 and H 2 only a few but dominant bush and tree species are found (Fig. 5). The two tree species *Ficus ingens* and *Maerua triphylla* contributed over half the plant biomass in kopje PH 2 and formed 90% of food eaten in the dry season. In kopje H 2 practically only one bush, *Grewia fallax*, regularly provided browse material, accounting for threequarters of the total feeding time in both seasons.

b) *Preference for certain plants* may cause a consumption increase out of proportion to vegetation density (Table 2). For instance, this was apparent for the bush *Cordia ovalis* in kopje H 1, or the tree *Maerua triphylla* in kopjes PH 1 and

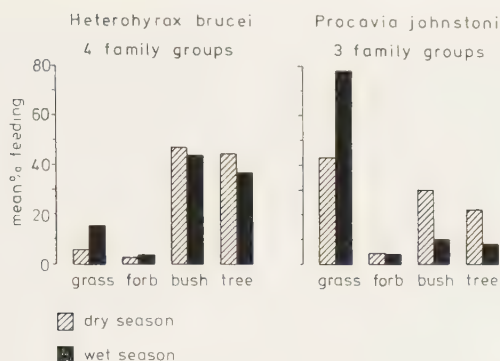


Fig. 11. Histogram of the percentage of time spent feeding on each of the four vegetation classes for the wet and dry seasons. Mean values of all four *H. brucei* and all three *P. johnstoni* family groups. Each group of four columns representing a season equals 100%

PH 2. All had low foliage density but were heavily browsed by the animals. Apparently such preferences are greatly influenced by the “optimal location” of the plant on the one hand and its *stage of development* on the other, *i.e.*, the presence of much-relished buds, young leaves, flowers or fruit. *Hibiscus lunariifolius* and *Maerua triphylla* for example are greatly favoured because of their fruit and flowers.

In the dry season, however, the animals must and will feed on coarser material such as old leaves, twigs or even bark. The fig tree (*Ficus* sp.) is a typical dry season stopgap; when food is scarce the hard leaves, containing a bitter latex, are eaten. The fruit is always eaten avidly.

Preferred plant species are regularly and systematically cropped by most members of a family group simultaneously (see section B) until very little edible material is left. The animals then move to another part of the kopje, or to an adjacent kopje, and continue feeding there from preferred bushes and trees.

b) P. johnstoni: *P. johnstoni* was observed feeding from 79 plant species (see Annex A).

Fig. 9 shows the foliage density percentage of the four vegetation classes and the feeding percentage (mean values of dry and wet seasons) of the three *P. johnstoni* family groups. As for *H. brucei*, a high correlation ($r_s = 0.88$, $P < 0.01$) is found between the feeding and the foliage density percentages, if grasses are excluded.

The animals thus fed more or less in proportion to the browse material (forb, bush and tree) growing on the kopjes. If grass is included the correlation vanishes ($r_s = 0.52$, $P > 0.05$), as the animals have a strong preference for grass, particularly striking in the wet season.

This makes for *strong seasonality* in this species as Fig. 10 shows: in the wet season food is mainly grass, in the dry season it is browse material.

Seasonal food differences were significant ($P < 0.001$; $df = 1$; $\chi^2 = 26$ (PH 1); $\chi^2 = 27$ (PH 2); $\chi^2 = 124$ (P 1)) for all three family groups.

To graze, *P. johnstoni* must go outside the kopje. Feeding areas around kopjes may become very obvious, as the grass is regularly and systematically cropped



Fig. 12. Feeding area of *P. johnstoni* (kopje P 1) at the edge of the kopje. Note the sharp border-line between short and long grass

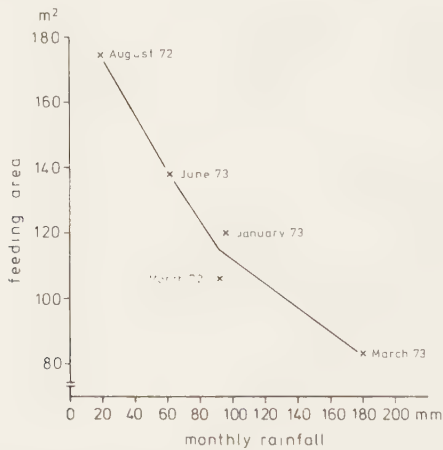


Fig. 13. Relation between feeding area size of *P. johnstoni* (kopje P 1) and monthly rainfall

until it resembles a lawn. Such an area (kopje P 1 in Fig. 12) tends to shrink in the wet season with high grass productivity and expand with decreasing rainfall (Fig. 13).

In the dry season when grass becomes parched and tough and poor in nutrients or even burnt the animals find their food on bushes and trees. Table 2 shows bush and tree species fed upon by the different family groups, especially in the dry

Table 3. Levels of significance for the difference in *grazing* (grass eating) and *browsing* (forb, bush, tree-eating) for each family group compared with every other group. The diagonal separates wet season (above) and dry season (below)

Kopje	<i>Heterohyrax</i>				<i>Procavia</i>		
	PH 1	PH 2	H 1	H 2	PH 1	PH 2	P 1
<i>Heterohyrax</i>							
PH 1		***			***	***	***
PH 2	**		***	***	***	***	***
H 1	**				***	***	***
H 2		***	**		***	***	***
<i>Procavia</i>							
PH 1	***	***	***	***		***	
PH 2	***	***	***	***	*		***
P 1	***	***	***	***	*		

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

season. As soon as the first rains fall and grass sprouts, *P. johnstoni* returns to the grass feeding area to graze. As for *H. brucei* differences between the family groups were noticeable: a significant difference in grazing and browsing was found in the wet season between PH 2 and PH 1, PH 2 and P 1, and in the dry season between PH 1 and PH 2, PH 1 and P 1 (see Table 3).

Also here, *vegetation composition and preference for certain plants* may have been responsible for kopje specific differences:

The kopje P 1 family group had an especially hard time in the dry season, as there were hardly any trees, and the three common bush species (Fig. 5) drop their leaves early. The staple food at this time was the bark of the bushes *Iboza* sp. and *Hibiscus lunarifolius*.

The kopje PH 2 family group consumed less grass than the others in the wet season, perhaps because this is a drier part of the Park in the short grass plains, and grass was not as abundant as elsewhere.

Preference for certain browse plants are noticeable (Table 2). For instance, a preference for *Hibiscus lunarifolius* rather than *Hoslundia opposita* is apparent, and for *Maerua triphylla* rather than *Ficus* sp. If *P. johnstoni* was seen eating fig leaves, almost no other green was available.

Feeding data are also given (Fig. 10) for the tame free-living family group. In this special case no pattern of seasonal food preference was evident, as they always had green grass and ample water and were also given bananas, etc. However, as in all other family groups there was an overall predilection for grass.

A. 2.2. Interspecific Relations

Of the 90 plant species eaten by *H. brucei* and *P. johnstoni* 53 were common to both (see Appendix A). Thus there is a substantial similarity with respect to the vegetation utilized by both species. Yet in spite of this impressive overlap the species are distinctly different.

Fig. 11 gives the average time the four *H. brucei* and three *P. johnstoni* family groups spent feeding on each of the four vegetation classes for the dry and wet seasons.

Table 3 shows the levels of significance for the inter- and intraspecific differences in grazing and browsing in both seasons between family groups.

Between all family groups the interspecific differences in grazing-browsing are always highly significant in both seasons (Table 3).

The reason for these differences is that *H. brucei* shows an over-all preference for browse material at all times. *P. johnstoni* on the other hand has a distinct seasonality: in the wet season grass is the staple food, whereas in the dry season 57% of feeding time was spent in browsing.

In addition to the difference discussed there is another type of food segregation which is very apparent in observation but difficult to document: on several occasions it was observed that the lighter *H. brucei* browsed on parts of bushes and trees inaccessible to the nearly twice as heavy adult *P. johnstoni*. This suggests that a certain segregation for browse material may take place by body weight difference.

Considering the available evidence for food overlap and food segregation *competition for food* could occur especially in the dry season in places where the species live sympatrically, as scarcity causes both species to rely heavily on the same vegetation of bushes and trees.

If there is competition one might expect a discernible intraspecific difference in the feeding behaviour between allopatric and sympatric family groups, at least during the dry season. Table 3 shows that in both seasons the intraspecific differences in grazing-browsing are of variable significance, but there is no evidence for competition-induced displacement.

In *H. brucei* there is no significant difference in the dry season between the allopatric H 1 and sympatric PH 2, or the allopatric H 2 and the sympatric PH 1 family groups; nor for the wet season between H 1 and PH 1, H 2 and PH 1, or between the allopatric H 1 and H 2 family groups.

In *P. johnstoni* there is no significant difference in the dry season between the allopatric P 1 and the sympatric PH 2 family groups, nor in the wet season between P 1 and PH 1.

Although the number of family groups compared is small, these results suggest that the feeding pattern of one species is not significantly affected by the presence of the other species. Thus, with respect to ecological displacement, there is no evidence for food competition.

B.1. Daily Course of Feeding Activity

Generally the main feeding activities of *P. johnstoni* and *H. brucei* in both seasons are concentrated in the cooler hours of the day, that is the morning (7.30–9.30) and evening (15.30–18.30); the evening feeding maximum is always higher than the morning one (Fig. 14).

In the dry season the morning feeding peak for *P. johnstoni* is at 8.30, that of *H. brucei* at 7.30. In the wet season *P. johnstoni* has two small peaks at 8.30 and 13.30 but a very marked evening one setting in an hour earlier than in the dry

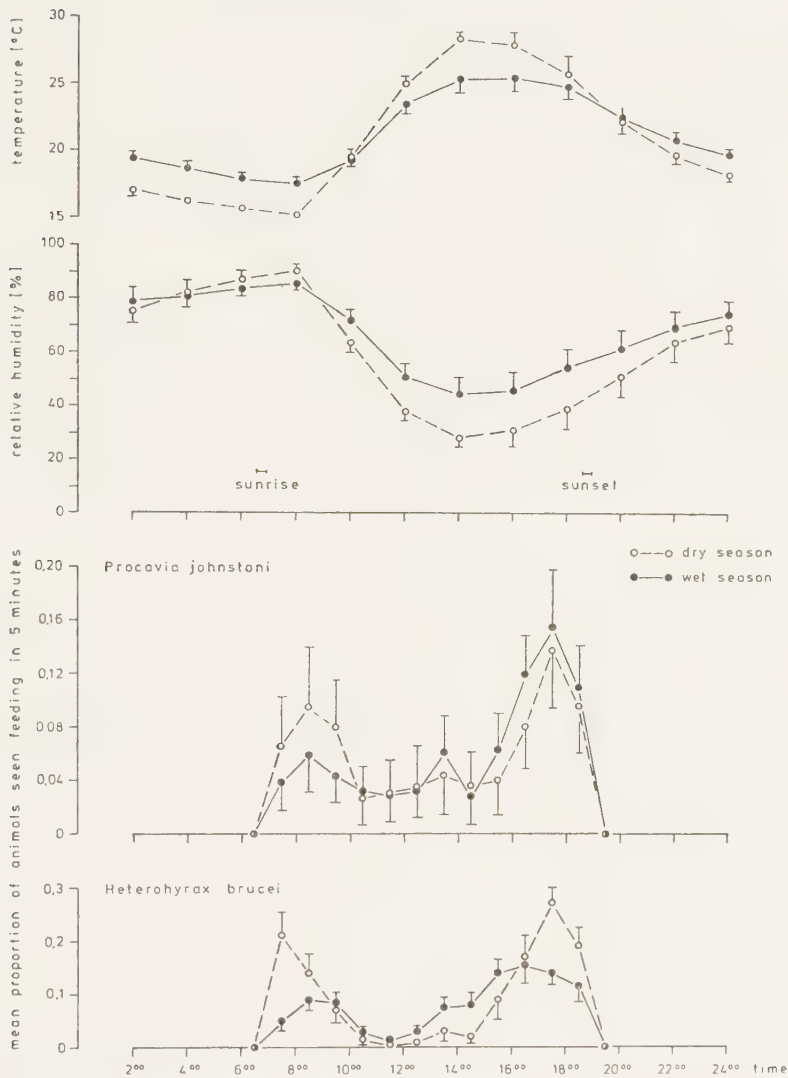


Fig. 14. The upper diagram shows the mean daily temperature (in °C) and relative humidity recorded with a thermohydrograph situated on top of a kopje in a box. The mean values are given for every 2 hrs with three times standard error. Dry season (5.6. to 16.9. 1972) values are given as open circles connected by a dotted line. Wet season (30. 10. 72 to 26. 3. 1973) values are given in solid circles connected by a continuous line. Lower diagram shows the feeding activities for *P. johnstoni* and *H. brucei*. The ordinate gives the mean proportion of animals seen feeding in a 5-min period every hour, with three times the s.e. Feeding data for *P. johnstoni* (dry season 41, wet 62 observation days), and the temperature and relative humidity data were collected at the same time. Observation days for *H. brucei* 10 in the dry and 21 in the wet season

season. For *H. brucei* the two peaks have a flatter and wider distribution, the morning maximum being around 8.30 and the evening increase commencing as early as 13.30. In the wet season the ratio between peaks for both species is more

pronounced than in the dry season and also (in contrast to the dry season) significantly different ($P = 0.028$ Mann Whitney U test). Thus there appears to be a shift towards evening feeding activity in the wet season.

In between the two feeding periods, when the temperature is highest and relative humidity lowest, most animals usually rest in the shade under bushes, trees or jutting rocks. Great heat may even cause retreat into the living holes. The animals do not feed while it is raining, and immediately vanish into their holes. On very cloudy days with constant drizzle they do not feed at all, but if the sun shines briefly they will immediately seize the chance to feed. The vegetation, especially grass, is always damp in the mornings in the wet season.

There are no apparent interspecific differences in the feeding activities save that in the dry season the feeding peak of *H. brucei* is an hour earlier than that of *P. johnstoni*, but this is not significant. Nor were any differences noticed on the two sympatric kopjes (PH 1, PH 2). Here animals of both species were often seen feeding at the same time from the same bushes or trees, especially in the dry season.

B.2. Social Feeding

B.2.1. Group Feeding

Feeding activity usually commences gradually: one member leaves the basking group and begins feeding, soon others follow, there is a movement into the feeding area and an intense period of group feeding starts.

An attempt was made to demonstrate to what extent such group feeding could be caused by environmental factors, by food clustering or by social stimuli.

a) *P. johnstoni*. In kopje P 1 a total of 307 animals was seen feeding in the wet season on the grass feeding area in 88 observation moments. The grass feeding area varied seasonally from 83 m² to over 180 m² (Fig. 13) and there was no noticeable difference in grass quality or density throughout the whole area. Yet 93% of the feeding animals were aggregated in groups (two or more animals, mean 3.9) within spaces not larger than 3 × 3 m. The location of the group feeding areas shifted during the course of the day, the whole area gradually being visited in this way: when the area was arbitrarily divided into about three equal subareas, group-feeding animals fed in these portions to 43–23–27%. If environmental components were responsible for the feeding aggregation, then one could have expected that the animals fed in a high percentage in one part of the area. Thus it may be concluded that the congregation of feeding animals in such small areas has social character.

b) *H. brucei*. Because of the heterogeneity of the food resources the social component of group feeding is more difficult to demonstrate for *H. brucei*: individuals may have a common preference for the growth stage and/or topographical location of particular bushes or trees. In addition, if the vegetation is sparse, as in kopjes H 2 and PH 2, the animals have little choice, they must necessarily feed in confined space on the few available bushes or trees. The large kopje H 1 was chosen for study of this aspect as it has numerous bushes and trees covering nearly half the area (see Table 1).

In 102 different observation moments, where two or more animals fed simultaneously, 311 animals were sighted. The distribution of the animals on the food

plants was not random: 77% of the observed animals were feeding together with others (mean group size 3.5) on the same plants (39% on a *Cordia ovalis* bush; 6% on an *Acacia tortilis* tree; 8% on a *Grewia fallax* bush; 18% on an *Hibiscus lunariifolius* bush and 6% on a *Maerua triphylla* tree) while 23% were feeding alone. These results suggest that in this species, too, group feeding on bushes and trees may have social character, or that at least a social component is involved.

B.2.2. Guarding

Very often, but not always, one or more adults will sit or lie on a high rock or branch and seem to observe while the other members of the group feed together. In order to test whether this guarding is random "not feeding" of random individuals, or a specific function of specific individuals, the situation was analyzed in two family groups of *P. johnstoni* and one family group of *H. brucei*. These three family groups were chosen as most individuals could regularly be seen at the same time. Fig. 15 gives the relative times in which at least one animal was seen eating and one not eating for *P. johnstoni* (tame animals and kopje P 1) and for *H. brucei* (kopje H 2).

In *P. johnstoni*, the individuals most frequently observed "not feeding" either solo (all other visible animals feeding) or not solo (some but not all other visible animals feeding) were the territorial ♂♂ No. 1 (tame animals) and No. 4 (kopje P 1). The quotients of solo/not solo of these ♂♂ are significantly ($P = 0.01$) higher than for any other member of their groups.

In *H. brucei* the situation is similar. Here the quotient solo/not solo of the territorial ♂ 3 of kopje H 2 is significantly ($P = 0.01$) higher than for the other members of the group.

From Fig. 15 it is also apparent that in all three studied family groups the territorial ♂♂ were seen feeding less frequently than the rest of the group. They move around more and rest or bask less often with the group than the other animals. This feature of the territorial ♂♂ is quite pronounced and significant in *P. johnstoni* while in *H. brucei* some of the adult ♀♀ behave similarly. It is not known whether the territorial ♂♂ actually feed less or feed at different times and/or parts of the kopje where they elude observation.

Thus during feeding, territorial ♂♂ can be distinguished from other animals in that they more often observe "solo" while all other members of the family group feed together.

B.3. Various Observations

P. johnstoni when leaving the kopje for the open immediately erects dorsal and neck hairs, exposing the dorsal gland (Sale, 1970b; Hoeck, in prep.). As already observed by Sale (1965b) they usually feed close together on the grass feeding area in a fan-like formation, each animal facing outward in a different direction. Especially the young regularly make contact calls which are answered by other members of the feeding group.

The guarding animals are often the first to give a warning or alarm call in case of sudden danger, whereupon the feeding animals take cover immediately.

When in association with the helmeted guinea fowl (*Numida mitrata*) the animals are less agitated while feeding, and venture further from the kopje.

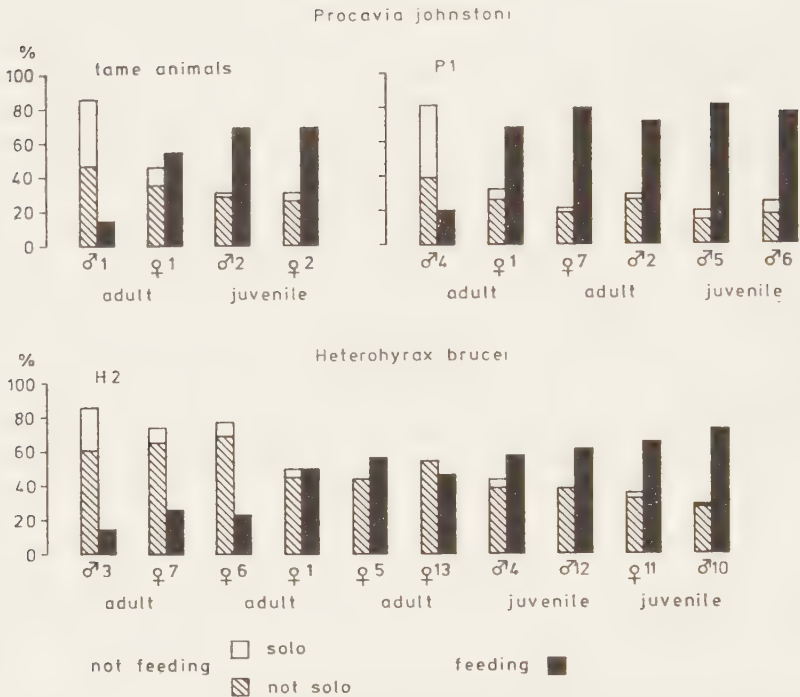


Fig. 15. All observation moments in which at least one animal was seen feeding and at least one animal was seen not feeding (excluded are all cases where all feed as well as where all do not feed). Given are the percentages for each individual *not feeding* (either solo or not solo) and *feeding*, for *P. johnstoni* two family groups: "tame animals" (8. 6. 72 to 15. 1. 73) and kopje P 1 (23. 9. 71 to 26. 3. 72); and for *H. brucei* kopje H 2 (30. 8. 71 to 28. 9. 72). Adults over, juveniles under 16 months. Each two columns add to 100%

H. brucei being mainly a browser stays mostly within the kopje. It is a very agile climber. No animal was ever observed to erect neck and dorsal hairs when feeding in tree or bush crowns nor while grazing outside the kopje.

In *sympatric kopjes* the young of both species browse together until *P. johnstoni* are 2–4 weeks old, when they accompany the adults into the grass feeding areas.

In the dry season, when adults of both species may feed together on the same bushes or trees, interspecific aggressive behaviour was seldom observed.

At group feeding times, individuals of both species may guard simultaneously: the warning or alarm call of either species is acted upon by all animals.

Discussion

Niche Overlap and Competition

My results do not support observations of Turner and Watson (1965) that the two species in Serengeti are completely separated in respect of feeding. These observations may have been confined to the wet season when indeed there is an almost complete separation, but dates were not given. The authors also report that

P. johnstoni does not browse on any of the plants which can be considered characteristic of kopjes, and that *Acacia tortilis* provides the bulk of *H. brucei*'s food, only kopjes where this tree grows being occupied by them. But according to my observations, when the grass becomes parched and lacks nutrients in the dry season, *P. johnstoni* has resource to considerable browsing on bushes and trees. Moreover, *A. tortilis* formed only a small proportion of the diet of all four *H. brucei* family groups.

Thus in the dry season *P. johnstoni* and *H. brucei* use practically the same food resources and occupy an almost identical niche. These results are in accordance with Sale's (1965a, b) observations on the allopatrically occurring *H. brucei hindei* and *P. habessinica* in Kenya. Unfortunately Sale makes no distinction between the food habits in the wet and dry seasons.

Both *P. johnstoni* and *H. brucei* can be classified, according to the Hofmann and Stewart (1972) characterization, as intermediate feeders, as they can adapt with the season or area to feed either on graze or browse material. But as my results show, *P. johnstoni* is mainly a grass eater while *H. brucei* is a browser. These results are supported for *Procavia* by the stomach analysis made by Coe (1962), and by differences in tooth structure (Lönneberg, 1916; Hahn, 1959). Molars and premolars of *Procavia* are hypsodont, *i.e.*, they have a high crown with relatively shorter roots, whereas *Heterohyrax* has brachydont tooth structure consisting of short crown and long roots. This suggests that *Procavia* feeds on coarser and *Heterohyrax* on softer material.

My results do not indicate any marked niche displacement when *P. johnstoni* and *H. brucei* occur on the same kopje. There was no discernible intraspecific difference in the feeding behaviour between sympatric (kopjes PH 1 and PH 2) and the allopatric (H 1, H 2, P 1) family groups. The situation is difficult to evaluate because kopje-specific differences of feeding are frequent whether the second species is present or not (Table 3). But there is no evidence that such differences are greater in sympatric kopjes.

Interspecific aggressive behaviour was seldom observed and there was no shift of feeding activity times due to the presence of the other species. In the dry season animals of both species were often seen browsing together on the same bush or tree.

These observations suggest that food material was always plentiful in both sympatric kopjes, even in the dry season when *P. johnstoni* turned to browsing and invaded the *H. brucei* food-niche. The studied kopjes (except PH 2) are situated in the northern and western wooded areas of the Park, where both species regularly occur sympatrically; the proximity of Lake Victoria causes relatively high rainfall with short drought periods. In most kopjes, therefore, food does not seem to be a limiting factor for the hyrax. Most family groups are probably limited by other physical factors (availability of optimal holes and cover, microclimate etc.), predation, diseases, intraspecific strife (territoriality of ♂♂) and inter-specific competition for holes (Hoeck, in prep.).

My observations do not exclude the possibility that food may sometimes be a limiting factor in prolonged droughts or in areas with low rainfall and limited browse material. This may explain the hyrax distribution throughout East Africa. As far as is known, the two Genera occur sympatrically only in the high

rainfall area around Lake Victoria. To the southeast of the Serengeti National Park in the Ngorongoro Conservation Area (Fig. 3) I hitherto always found allopatric tenancy of the kopjes and screes. The mean annual rainfall here is below 500 mm.

Food Selection and Feeding Time

As described, *P. johnstoni* and *H. brucei* are very comprehensive feeders. They were seen feeding on a great variety of different plant species (see Annex A), also observed by Sale (1960, 1965a, b, 1966) and Meltzer (1967). In this they resemble the related *Proboscidea* (Dougall and Sheldrick, 1964; Hendrichs, 1971; Croze, 1974) and *Sirenia* (Hartman, 1971). However, feeding is not unselective. *P. johnstoni* and *H. brucei* concentrated upon shoots, young tender leaves, flowers and fruits when food was plentiful, but when the dry season brought scarcity and lowered quality they ate coarser leaves, branches and bark. This is also reported by Hahn (1959), Sale (1960, 1965a, b), Meltzer (1967) and supports Emlen's prediction (1966) that animals should be more selective in choice of foods when satiated or when food is abundant, and less discriminating when famished or when food is scarce.

This selection is probably for food material rich in protein and energy. It is known that protein content is highest and fibrous tissue lowest in newly emerged or growing foliage, while old or dry foliage is highly lignified with very low protein content (Dougall and Bogdan, 1958; Dougall and Sheldrick, 1964; Dougall *et al.*, 1964; McKay and Frandsen, 1969; Roth and Osterberg, 1971; Bell, 1970, 1971; Braun, 1972). Crude protein percentage in dry matter is below 5% in grasses and above 5% for browse material in the dry season, while the wet season regrowth for grass and browse is 11–30% (Dougall *et al.*, 1958, 1964; McKay *et al.*, 1969; Braun, 1972). Braun (1972) also indicates that forage low in protein is low too in digestible energy, high protein content being linked with high energy content.

For several reasons the optimal feeding strategy of the hyrax should be to eat plants or plant parts rich in protein and energy content. Firstly, small-bodied animals require more energy and protein per day per unit weight than large animals (Bell, 1970). Secondly, by consuming newly emerged items rich in protein and energy content with low lignified material they minimize feeding time, which is beneficial because a) having poor homeothermic regulation (Taylor and Sale, 1959; Bartholomew and Rainey, 1971) hyrax must restrict their periods of activity to suitable times of the day, and b) while feeding they are especially vulnerable to predation. The individual daily feeding period is actually much shorter than the average values of Fig. 14 indicate, generally being no more than 1–2 hrs

The observed pattern of group feeding promotes homogeneous development of the vegetation which in turn increases cropping efficiency.

P. johnstoni, by feeding in groups and systematically cropping the grass (Fig. 12), prevents the growth of lignified material which would obscure new shoots and increase the searching time when the first rains fall. On the lawn-like cropping area the new shoots are readily available and evenly distributed. Similarly, *H. brucei*'s concerted browsing strategy on certain bush and tree species prevents the development of old, coarse leaves unpalatable with oils and resins.

When seasonal growth starts, the fresh young leaves are immediately accessible, unobscured by old foliage.

Grass growth decreases with too frequent clipping (Braun, 1972), and after intense grazing pastures need a rest (Vesey-FitzGerald, 1960). Therefore in order to maintain maximal leaf growth the animals should crop different feeding areas at regular intervals, which may explain the observed regular movements of family groups within a kopje or between closely located kopjes. These migratory movements were also observed by Sale (1965b) and Meltzer (1967).

In the dry season the grasses are the first to stop growing and become parched, with little protein and energy content, but some bushes and trees still retain leaves with higher nutritional values. A switch to browsing, then, is to *P. johnstoni*'s advantage. The proportion of palatable food decreases in the course of the dry season, and *P. johnstoni* and *H. brucei* must fall back on progressively coarser material such as fig tree leaves, or even bark. This stops immediately with the onset of the first rains, as also observed by Sale (1965b). As soon as the grasses started growing *H. brucei* was very often seen grazing together with *P. johnstoni* until the forbs, bushes and trees also sprouted, when *H. brucei* returned to browsing.

Other Food Competitors

Other animal species also feed on the kopje and are possibly food competitors of the hyrax. In Appendix A are listed some animal species that were observed feeding regularly from plant species eaten by *P. johnstoni* and *H. brucei*.

The two most likely food competitors are the giraffe (*Giraffa camelopardalis*) and the elephant (*Loxodonta africana*). The former browses regularly in some kopjes on the crowns of bushes and trees also browsed by both hyrax species. The latter visits the kopjes, especially in the dry season, and feeds on many plant species, breaking branches and uprooting bushes and so changing the habitat.

Appendix A

List of Plants Eaten by *Procavia johnstoni* and *Heterohyrax brucei* in the Serengeti National Park

Abbreviations. B = twig or bark; L = leaf or shoot; F = flower; f = fruit.

Food Competitions

- 1 Dik-Dik (*Rhynchotragus kirki*)
- 2 Giraffe (*Giraffa camelopardalis tippelskirchi*)
- 3 Elephant (*Loxodonta africana*)
- 4 Lizard (*Agama planiceps mwanzae*)
- 5 Love bird (*Agapornis fischeri*)
- 6 Red-billed hornbill (*Tockus erythrorhynchus*)
- 7 Green pigeon (*Treron australis*)
- 8 Ruppell's long tailed glossy starling (*Lamprocolius chalybaeus*)
- 9 Bare-faced go-away-bird (*Gymnoschizorhis personata*)
- 10 Brown parrot (*Poicephalus meyeri*)
- 11 Yellow-vented bulbul (*Pycnonotus xanthopygos*)

	<i>Pro.</i>				<i>Het.</i>				Other common feeders
	B	L	F	f	B	L	F	f	
Acanthaceae									
<i>Blepharis acanthooides</i> Klotz			×						3 ^a
<i>Hypoestes forskalii</i> (Vahl) R.Br.			×	×			×		
Adiantaceae									
<i>Pellaea calomelanos</i> (Sw.) Link.			×						
Agavaceae									3 ^a
<i>Sansevieria ehrenbergiana</i> Schweinf.			×				×	^b	1 ^a , 3
<i>Sansevieria suffruticosa</i> N.E.Br.			×				×		
Amaranthaceae									
<i>Achyranthes aspera</i> L.			×						1 ^a
<i>Pupalia lappacea</i> (L.) Juss.			×				×	×	
Anacardiaceae									
<i>Sclerocarya birrea</i> (A.Rich.) Hochst.			×				×		3 ^a
Balanitaceae									
<i>Balanites aegyptiaca</i> (L.) Del.							×	×	3 ^a , 2
Boraginaceae									
<i>Cordia ovalis</i> R.Br.			×	×			×	×	1 ^a , 3 ^a , 9
<i>Heliotropium steudneri</i> Vatke							×		
Burseraceae									
<i>Commiphora schimperi</i> (Berg.) Engl.			×	×			×	×	3, 5, 9
<i>Commiphora merkeri</i> Engl.							×		3
Caesalpinaceae									
<i>Cassia didymobotrya</i> Fres.			×	×	×		×	×	
Capparaceae									
<i>Capparis tomentosa</i> Lam.			×				×	×	1 ^a , 3 ^a
<i>Maerua triphylla</i> A. Rich.			×	×	×		×	×	1, 2, 3 ^a , 4, 6
Combretaceae									
<i>Combretum molle</i> R. Br. ex G. Dom			×						
Commelinaceae									3 ^a
<i>Commelina africana</i> L.			×	×	×		×	×	1 ^a , 4
Compositae									
<i>Emilia coccinea</i> (Sims) Sweet			×	×			×		
Convolvulaceae									
<i>Ipomoea obscura</i> (L.) Kers.			×				×		
Crassulaceae									
<i>Kalanchoe</i> sp.							×	×	1 ^a
Cucurbitaceae									
<i>Kedrostis foetidissima</i> (Jacq.) Cogn.			×				×		
Cyperaceae									
<i>Cyperus kilimandscharicus</i> Kukenth. e. desc.			×	×					
<i>Cyperus</i> sp.			×						
<i>Kyllinga nervosa</i> Steud.			×						

	Pro.				Het.				Other common feeders
	B	L	F	f	B	L	F	f	
Euphorbiaceae									
<i>Acalypha fruticosa</i> Forsk.									
var. <i>villosa</i> Pax.			×				×		1 ^a , 3 ^a
<i>Croton dichogamus</i> Pax.			×				×		3 ^a
<i>Phyllanthus sepialis</i> Muell. Arg.	×	×	<		×	×			3 ^a , 2
Gramineae									
<i>Aristida adoensis</i> A. Rich.							✓		
<i>Aristida hordaecea</i> Kunth.			×						
<i>Aristida kenyensis</i> Henr.									1 ^a
<i>Botriochloa insculpta</i> (A. rich.) A. Camus			×						
<i>Brachiaria semiundulata</i> (Hochst.) Stapf.									
<i>Cenchrus ciliaris</i> L.			×						1 ^a
<i>Chloris pycnothrix</i> Trin.			×						
<i>Cynodon dactylon</i> (L.) Pers.							✓		
<i>Digitaria macroblephara</i> (Hack.) Stapf.			×						
<i>Digitaria ternata</i> (A. Rich.) Stapf.			×						
<i>Digitaria velutina</i> (Forsk.) Beauv.							<		
<i>Diheteropogon amplexans</i> (Nees) W. D. Clayton			×						
<i>Eragrostis aspera</i> (Jacq.) Nees			×						
<i>Eragrostis tenuifolia</i> (A. Rich.) Steud.			×						1 ^a
<i>Eriochloa nubica</i> (Steud.) Thell			×						
<i>Heteropogon contortus</i> (L.)			×				✓		1 ^a
<i>Microchloa kunthii</i> Desv.			×						
<i>Panicum maximum</i> Jacq.			×	×	×			×	1 ^a
<i>Pennisetum mezianum</i> Leeke			×						
<i>Pennisetum stramineum</i> Peter			×				×		
<i>Sporobolus pellucidus</i> Hochst.			×						
<i>Sporobolus stapfianus</i> Gand.			×						
<i>Themeda triandra</i> Forsk.									
var <i>hispida</i> (Nees) Stapf.							✓		
<i>Tricholaena eichingeri</i> (Mez.) Stapf & Hubbard							✓		
Labiatae									
<i>Hoslundia opposita</i> Vahl.			×	×	×		×	×	1
<i>Iboza</i> sp. Greenway 10,315 10,350	×		×	×					3
<i>Ocimum suave</i> Willd.			×				✓		1 ^a
Liliaceae									
									5 ^a
<i>Albuca</i> sp.			×	×			×		4
<i>Aloe macrosiphon</i> Bak.			×	×			×		1 ^a
<i>Aloe secundiflora</i> Engl.			×				×		
Malvaceae									
<i>Abutilon angulatum</i> (Guill. & Perr.) Mast.			×				✓		3 ^a
<i>Hibiscus aponeurus</i> Sprague Hutch.			×	×			✓		1 ^a
<i>Hibiscus cannabinus</i> L.			×	×					
<i>Hibiscus flavifolius</i> Ulbr.			×	×			×		1 ^a
<i>Hibiscus lunarifolius</i> Willd.	×		×	×			×	×	1 ^a , 2, 3, 4
<i>Pavonia patens</i> (Andr.) Chiov.			×				×		
Meliaceae									
<i>Turreae fischeri</i> Guerke			×	×	×		×	×	

	<i>Pro.</i>				<i>Het.</i>				Other common feeders
	B	L	F	f	B	L	F	f	
Mimosaceae									3 ^a
<i>Acacia clavigera</i> E. Mey. ssp.									
<i>usambarensis</i> (Taub.) Brenan			×			×		×	
<i>Acacia tortilis</i> (Forsk.) Hayne ssp.									2, 3
<i>Spirocarpa</i> (Hochst. ex A. Rich.) Brenan			×			×	×	×	
<i>Albizia harveyi</i> Fourn.			×	×		×		×	
Moraceae									3 ^a
<i>Ficus glumosa</i> Del. (Syn. <i>F. sonderi</i> Miq.)			×	×		×		×	1 ^a , 3, 5, 6, 7, 8, 9, 11
<i>Ficus ingens</i> Miq.		×	×	×		×		×	3, 5, 6, 7, 8, 11
<i>Ficus thonningii</i> Blume						×	×		4
Olacaceae									
<i>Ximenia caffra</i> L.			×			×			3 ^a
<i>Jasminum fluminense</i> Vell. ssp.									
<i>holstii</i> (Gilg) Turrill			×	×		×			
Papilionaceae									
<i>Indigofera basiflora</i> Gillett						×			1 ^a , 3 ^a
Rhamnaceae									
<i>Zisiphus mucronata</i> Willd.						×			3 ^a
Rubiaceae									
<i>Pavetta assimilis</i> Sond.			×			×	×	×	3, 2
Sapindaceae									
<i>Allophylus rubifolius</i> (Hochst.) Engl.			×			×		×	1 ^a , 3 ^a
<i>Pappea capensis</i> Eck & Zey.			×			×			3 ^a
Solanaceae									3 ^a
<i>Solanum dennekense</i> Dammer			×			×			1 ^a
<i>Solanum incanum</i> L.			×						1 ^a
<i>Solanum nigrum</i> L. sl			×	×					1 ^a
<i>Solanum</i> sp. = Greenway 9086			×			×			
Tiliaceae									3 ^a
<i>Grewia fallax</i> K. Schum.			×			×	×	×	3, 4, 9, 10
<i>Grewia trichocarpa</i> A. Rich.			×			×	×	×	1, 2, 3, 8
Verbenaceae									
<i>Lippia</i> sp.						×			3 ^a
<i>Lippia ukambensis</i> Vatke						×			
Vitaceae									
<i>Cissus quadrangularis</i> L.		×	×			×	×		3 ^a , 4
<i>Cissus rotundifolia</i> (Forsk.) Vahl.			×			×			3 ^a , 4
<i>Cyphostemma nierenensis</i> (Th. Fries) Desc.									
(Syn. <i>Cissus nierenensis</i> Th. Fries)			×			×	×		
<i>Rhoicissus revoilii</i> Planch.			×						3 ^a

^a Data from Hendrichs and Hendrichs (1971).^b Roots.

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Lebenslauf

Am 18.1.1944 wurde ich als Sohn von Dr.ing.H. Hoeck und seiner Ehefrau Dr.phil.D.Hoeck, geb. Meyer, in Bogotá, Kolumbien, geboren. Ich bin kolumbianischer Staatsangehöriger.

Nach jeweils sechsjährigen Besuch der Vor- und Oberschule im "Colegio Andino" (Deutsche Schule) legte ich an dieser Anstalt im Jahre 1961 die kolumbianische Reifeprüfung ab. Im Oktober 1962 bestand ich am Studienkolleg der Universität Bonn die Prüfung der Hochschulreife ausländischer Studierender. Anschliessend machte ich ein Praktikum bei der Firma BBikow Entwicklungen und studierte zwei Semester Maschinenbau an der Technischen Hochschule München. Im November 1964 kehrte ich nach Kolumbien zurück, arbeitete im Betrieb meines Vaters und studierte nebenbei an der dortigen Universität Biologie. Im Wintersemester 1965 begann ich mit dem Studium der Biologie an der Universität München und legte dort im Juni 1970 die mündliche Diplomprüfung ab. Ende 1970 ging ich mit der Unterstützung des Max-Planck-Institutes, Seewiesen, in die Serengeti nach Tanzania, um dort die Ökologie und das Verhalten des Klippschliefer Procavia johnstoni und des Buschschliefer Heterohyrax brucei zu untersuchen. Im August 1973 kehrte ich nach Deutschland zurück und begann mit der Ausarbeitung der Freilandbeobachtungen.

